

# **FOREST SUCCESSION AND STAND DEVELOPMENT RESEARCH IN THE NORTHWEST**

Proceedings of the Symposium held 26 March 1981  
as part of the Northwest Scientific Association annual meetings  
at Oregon State University, Corvallis.

Co-sponsors: Northwest Scientific Association  
Pacific Northwest Forest and Range Experiment Station,  
USDA Forest Service  
School of Forestry, Oregon State University

Joseph E. Means, editor

Published June 1982  
Forest Research Laboratory, Oregon State University, Corvallis, Oregon 97331

Price \$6.00

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MODELING LONG-TERM FOREST SUCCESSION  
IN THE PACIFIC NORTHWEST

by

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and

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ABSTRACT--A computer model has been developed to simulate forest succession in western Oregon and Washington based on models for other geographic locations. The model tracks the birth, growth and death of individual trees in a forest gap. Birth is random for species able to grow in the existing shade condition. Species-specific diameter increment is dependent on tree diameter, existing foliage biomass, temperature and moisture effects upon growth, competition and shade tolerance. Slow-growth related mortality is conditioned by the size of the tree and the successional status of the species. The results of simulations for xeric and mesic sites in Oregon compare well to species composition and tree size measured in representative forests of each moisture type. Model development suggested parameters which are likely to have major effects on forest succession but which have not been measured in forests as the species composition changes over time. The model is particularly useful for long-term analysis of the effects of disturbances.

KEYWORDS--simulation, mortality, diameter increment

CLIMACS (Computer Linked Integrative Model for Assessing Community Structure) is a model of tree succession for the coniferous forest of western Oregon and Washington. By tracking long term changes in species composition the model can be used to study the effects on forest succession of different disturbances (fire, wind, clearcuts or herbivory), climatic changes and management strategies. In this paper we describe the model emphasizing differences from other succession models and present results from the model based on xeric and mesic habitats of western Oregon.

A recent review of forest succession models (Shugart and West 1980) discusses 3 major types of models available: gap, tree, and forest models. We chose to use a gap model which allows long term tracking of individual trees and does not use excessive computer time. Tree models follow the dynamics of a single tree and can become extremely complicated as demonstrated by the work of Ek and Monserud (1974). Forest models consider the entire stand as the central point of focus, and thus the actual mechanisms of species changes are not included.

CLIMACS is based upon FORET, a model of forest succession in eastern Tennessee, (Shugart and West 1977; Mielke et al. 1978) which, in turn, is a modification of JABOWA, developed for northeastern deciduous forests (Botkin et al. 1972). The prime differences between this model and its forerunners are the elaboration of the diameter increment equation and a more sophisticated treatment of mortality. In addition to incorporating size effects, foliage biomass, temperature, nutrient competition and shade tolerance, the diameter increment function in CLIMACS includes a moisture stress index. Also height growth is dependent upon site quality as well as species. Mortality is considered in terms of 5 groups of species dependent upon the successional status and the ability to endure suppression.

The model tracks characteristics of individual trees of 21 potential species growing in a fifth hectare

forest gap. The model considers spatial relationships in the vertical dimension (leaf area is calculated for 1-dm height classes and affects the probability of birth and death) but not in the horizontal dimension (Cartesian coordinates of a tree are unknown). State variables of the system are the diameter at breast height, the age and species of each tree; the total aboveground biomass, foliage biomass and projected leaf area for each species; the number of trees in 16 diameter classes for each species; and the stand biomass, the leaf area index and the basal area.

The driving variables for the model are plant moisture stress (negative water potential) and temperature growth index. Plant moisture stress is the predawn xylem pressure measured at the end of the growing season and serves as an integrator of factors affecting available soil moisture throughout the year (Zobel et al. 1976). The temperature growth index is from a temperature summing formula which weights temperatures by their effect on productivity of Douglas-fir seedlings (Cleary and Waring 1969). Together, plant moisture stress and temperature growth index reflect the major environmental factors affecting tree growth and serve to characterize a habitat (Zobel et al. 1976).

The model is applicable to four geographic regions in western Oregon and Washington: south of Santiam Pass to the California border, Santiam Pass to Snoqualmie Pass, Snoqualmie Pass to the Canadian border, and the Olympic Peninsula. Only species that occur within a given geographic zone can enter a plot within that region.

The three major subroutines of the fortran program will be discussed in detail in this paper. BIRTH stocks the plot with 10 to 15 cm diameter trees; GROW calculates the diameter increment for each tree; and KILL causes mortality to occur.

#### SUBROUTINE BIRTH

The BIRTH subroutine introduces a random number of young trees from the eligible species pool into the plot. It proceeds until the projected leaf area for the plot exceeds  $1.0 \text{ m}^2/\text{m}^2$ , resulting in full stocking the first year of the model run. This means that model year 1 does not correspond to year 1 of a stand. The species selected for possible introduction are those which can survive and grow under the existing water stress, temperature range and soil in the geographic region under consideration. Actual entry into the plot is conditioned by the projected leaf area of the existing trees and the relative shade tolerance of the entering species. On the first year any species can enter the plot. Thereafter, if the projected leaf area is greater than  $3 \text{ m}^2/\text{m}^2$ , *Alnus rubra*, *Pinus ponderosa* and *Arbutus menziesii*, the most intolerant species, cannot enter. If the projected leaf area exceeds  $10 \text{ m}^2/\text{m}^2$  then only the most tolerant species, *Abies amabilis*, *A. grandis*, *Castanopsis chrysophylla*, *Calocedrus decurrens*, *Chamaecyparis nootkatensis*, *Thuja plicata*, *Tsuga heterophylla* and *T. mertensiana*, can enter the plot. Since trees enter the plot at 10 to 15 cm DBH, this limitation means that only select species can germinate and survive in the shade conditions, not that the other species cannot germinate.

Projected leaf area is a function of total stand foliage biomass and is related to the diameter of each

tree of a given species. The equations for foliage biomass are from Gholz et al. (1979) for trees less than 50 cm in diameter. Since diameters larger than 50 cm exceed the data range of the Gholz equations, we used the following indirect method to estimate the foliage biomass of large trees. The foliage biomass for *Pseudotsuga menziesii* is calculated from the relationship between diameter, sapwood area, and foliage biomass (R. Waring personal communication, Figure 1). This relationship is multiplied by the ratio of the foliage biomass for a 50 cm tree of the species being considered to that of a 50 cm *Pseudotsuga menziesii*, as estimated from Gholz et al. (1979). All of the foliage biomass is considered to be at the tip of the tree. This umbrella-like shading causes tall trees to have a great influence on the understory trees.

The height to diameter equation is parabolic (as recommended by Ker and Smith 1955). For most species the parameters of the height equation are based upon those used by Botkin et al. (1972). Since height and diameter data were available for *Pseudotsuga menziesii*, *Abies procera*, *A. amabilis*, *Tsuga heterophylla*, *T. mertensiana* and *Thuja plicata* from the H. J. Andrews Experimental Forest, the parameters for these species were found by regression analysis ( $R^2 = .96$  in all cases) (see Adams and Hemstrom 1982 for a complete discussion).

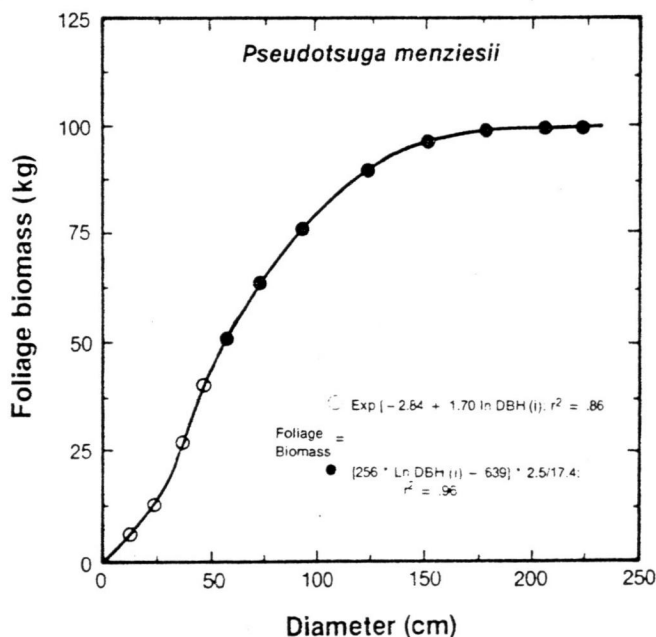


FIGURE 1. Foliage biomass as related to diameter for *Pseudotsuga menziesii*.

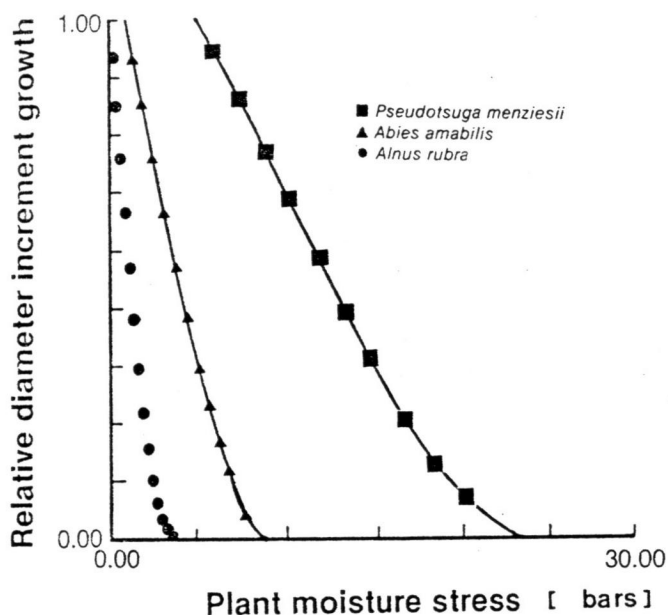


FIGURE 3. Index of the effects of moisture stress on the relative growth rates of three species used in CLIMACS.

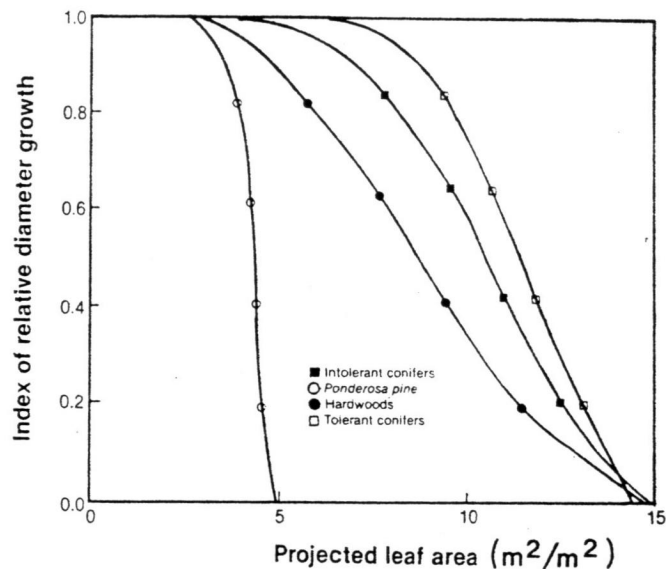


FIGURE 4. Index of the relative diameter growth as a function of projected leaf area used in CLIMACS.

(5) competition

$$1 - \text{SBIO}/\text{SOILQ} ;$$

(6) shade tolerance (Figure 4)

$$1 - \exp(-a_1(AL-a_2))$$

where  $a_1$  and  $a_2$  are species specific parameters. Available light is dependent upon the total foliage leaf area of all trees taller than the one being considered.

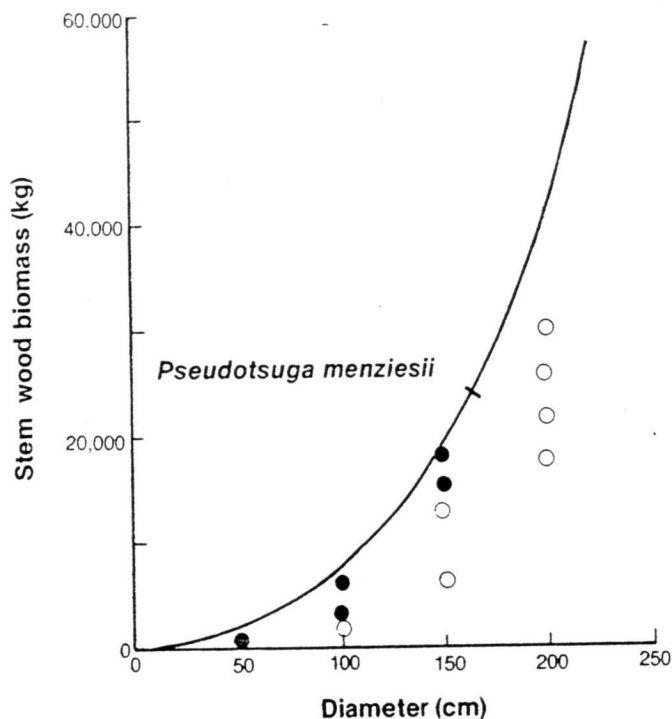
The factor for competition is dependent upon total above ground biomass (SBIO) which is obtained from the addition of stem wood and foliage biomass. The stem wood biomass is based on the equations of Gholz et al. (1979). Since large trees exceed the data range used by Gholz et al., there may be errors in stemwood biomass estimates for trees over 50 cm in diameter. For most species, e.g., *Pinus ponderosa* (Fig. 5) and *Calocedrus decurrens* (Fig. 6), the equations of Gholz et al. fit large trees well. The stem biomass values for large trees in Figures 5, 6, and 7 were estimated by multiplying stem volume (MacLean and Berger 1976) times wood density (U.S. Forest Products Laboratory 1974). Based on this data, the *Pseudotsuga menziesii* equation overestimates stem biomass of large trees (Fig. 7). However, in the absence of actual biomass data from large trees, we used the only available equations (Gholz et al. 1979).

Since the diameter increment equation is a multiplicative function of six factors (all ranging from 0 to 1), it is most influenced by the smallest factor. If the diameter increment for a tree is less than 1 mm that tree is subjected to potential slow-growth-related mortality.

#### SUBROUTINE KILL

The probability of non-catastrophic mortality is calculated for each tree based on its diameter and diameter growth rate, the maximum diameter for the species and the successional status of the species. The mortality equations are derived from stand densities of various ages from McCardle et al. (1949) and unpublished data from a chronosequence of stands in the Washington and Oregon Cascades.

For short-lived seral species such as *Alnus rubra* or *Quercus garryana* the annual probability of slow-growth-related mortality is 0.628. For all other successional classes the mortality changes with diameter of the tree (Figure 8). Long-lived early seral species have decreasing mortality until 20% of the maximum diameter is reached when the probability of slow-growth-related mortality becomes constant. Late seral species have slightly decreasing mortality until 10% of the maximum diameter is attained when the probability begins to increase. For long-lived, mid-seral species the probability of slow-growth-related mortality remains low and nearly



*Pseudotsuga menziesii* is also the dominant tree on the mesic sites. After 400 years of simulation one large *Pseudotsuga menziesii* is left on the fifth hectare plot and has a major influence on regeneration and growth because of its large size. The earlier death of the other dominant *P. menziesii* (by slow-growth-related mortality) resulted in the release of suppressed understory and lower canopy *Tsuga heterophylla* (Figure 9). Small trees of *Abies grandis*, *Calocedrus decurrens* and *Castanopsis chrysophylla* also occur on the simulated mesic plot as well as at the H. J. Andrews Experimental Forest. After 400 years the leaf area of the simulated stand is 16.9 compared to 15.2 m<sup>2</sup>/m<sup>2</sup> on a 450-year-old natural stand measured in the H. J. Andrews Experimental Forest. Given the variability of natural ecosystems the model results compare well to data on the reference stands.

Leaf area gives an indication of stress for understory trees resulting from shading and age of the stand. There are no data available documenting changes in the leaf area of a stand over time, but the model projects a maximum to be reached late in the stand history for both xeric and mesic habitats (Figure 11). The densest canopy is attained near simulation year 400.

FIGURE 7. Stem wood biomass as related to diameter for *Pseudotsuga menziesii* used in CLIMACS. See note with Fig. 5 caption for explanation of symbols.

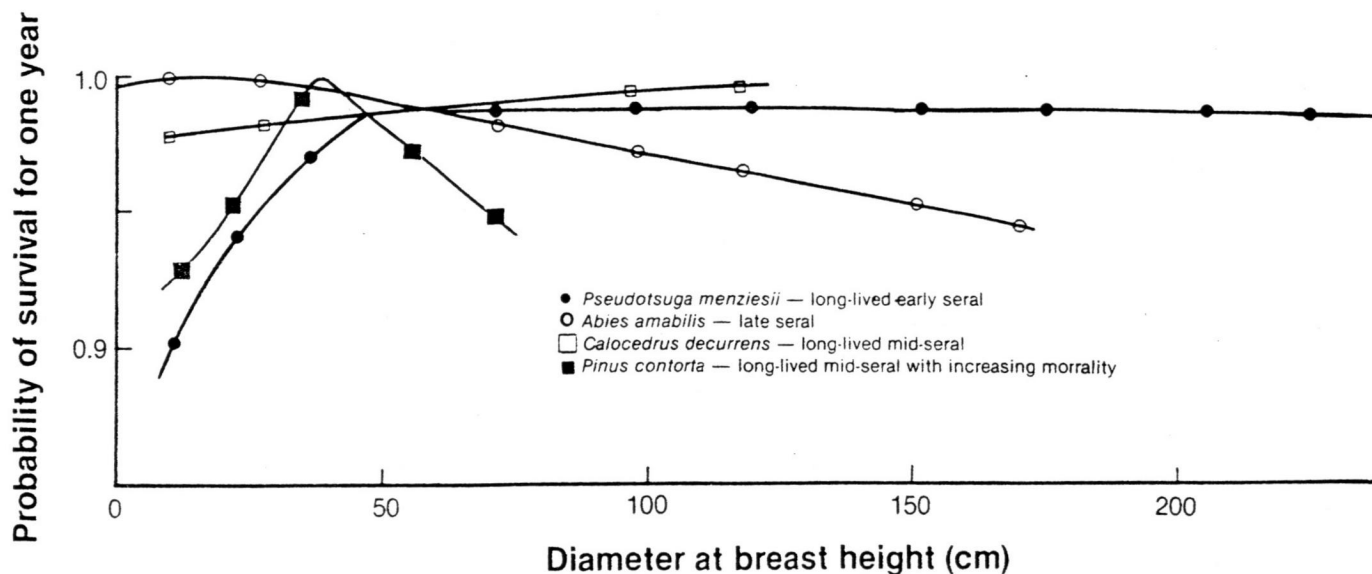


FIGURE 8. Probability of surviving one year of slow growth for four successional classes. A fifth class, short-term early-seral species, has a constant survival probability of 0.628.

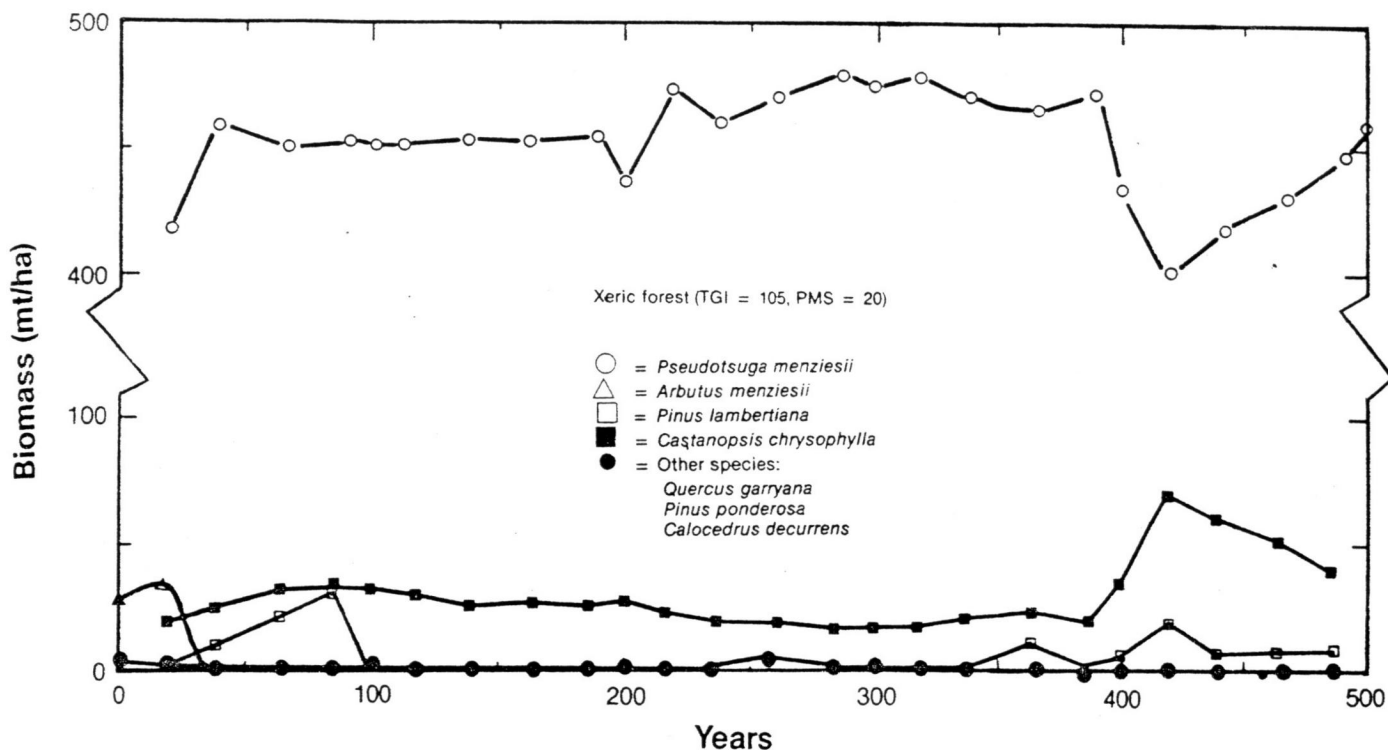


FIGURE 10. Predicted total aboveground biomass by species over a 500 year simulation on a xeric site. Since the trees are introduced at 10 to 15 cm DBH the first few years are not comparable to natural stands.

TABLE 1.

SIMULATED MODEL CHARACTERISTICS FOR XERIC AND MESIC STANDS COMPARED TO DATA FROM THE H. J. ANDREWS EXPERIMENTAL FOREST (FROM WARING ET AL. 1978; FRANKLIN AND WARING 1980; AND HAWK ET AL. 1978).

Source of Data	Plant Moisture Stress (- bars)	Temperature Growth Index (days)	Age (years)	Projected Leaf Area (m <sup>2</sup> /m <sup>2</sup> )	Basal Area (m <sup>2</sup> /h)	Foliage Biomass (mt/h)
Natural Xeric Stand <sup>a</sup>	20	102	450	9.4	72.5	14
Simulated Xeric Stand	20	105	460	10.3	68.0	15
Natural Mesic Stand <sup>b</sup>	11	84	450	15.2	98.6	18
Simulated Mesic Stand	11	84	400	16.9	84.9	21

Source of Data	Number of <i>Pseudotsuga menziesii</i> per hectare in each diameter class (cm)												
	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	100-110	110-120	120-130	130+
Natural Xeric Stand <sup>a</sup>	96	52	16	12	16	12	4	12	16	4	8	8	8
Simulated Xeric Stand	0	0	25	20	15	5	25	10	10	10	0	0	5
Natural Mesic Stand <sup>b</sup>	0	0	0	0	0	4	8	12	4	12	12	8	20
Simulated Mesic Stand	0	0	0	0	0	0	0	0	0	0	0	0	5

<sup>a</sup>Reference Stand 1

<sup>b</sup>Reference Stand 2

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## APPENDIX

### List of Symbols

#### Indices:

j = 1, ..., NTOT = tree number

i = 1, ..., NSPEC = species number

#### Parameters:

AL = available light

B1(i) = coefficient relating tree volume growth to leaf biomass

B4(i) = exponent relating tree volume growth to leaf biomass

DEH(j) = diameter at breast height of tree j (cm)

DBHMX(i) = maximum diameter for species i (cm)

DMIN(i) = minimum number of degree growing days for species i (days)

DMAX(i) = maximum number of degree growing days for species i (days)

HMAX(i) = maximum height for species i (cm)

HT(j) = calculated height of tree j (cm)

NSPEC = total number of species

NTOT = total number of trees

SBIO = total above ground biomass (kg)

SOILQ = maximum biomass a fifth hectare plot can support (kg)

#### Driving Variables:

PMS = plant moisture stress (negative bars)

TGI = temperature growth index (days)

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